Feeding preferences of supralittoral isopods and amphipods

Steven C. Pennings, Thomas H. Carefoot, Martin Zimmer, Jean Paul Danko, and Andreas Ziegler

Abstract: We examined the feeding preferences of 3 supralittoral crustacean species in the Pacific Northwest of North America. The isopod Ligia pallasii (Brandt, 1833), the rocky-shore amphipod Traskorhychia traskana (Stimpson, 1857), and the sandy-beach amphipod Megarhychia californiana (Brandt, 1851) had similar feeding preferences, suggesting that feeding preferences were based on general algal traits rather than on adaptations particular to specific herbivores. No single trait clearly distinguished low- and high-preference seaweeds, although pH and phenolic compounds may have been important for two chemically defended seaweeds (Desmarestia sp. and Fucus sp., respectively). Feeding preferences of L. pallasii were affected by dietary history, but effects were minor compared with differences among seaweeds. All 3 consumers tended to prefer wrack (aged, stranded seaweeds) over fresh seaweeds of the same species. Our results suggested that increased organic and mineral contents of wrack were important in mediating these preferences, but that toughness and salt and nitrogen contents were not. Reduced levels of defensive compounds may have made wrack more palatable than fresh seaweeds in the case of the two chemically defended seaweeds.

Résumé : Nous avons étudié les préférences alimentaires de 3 crustacés de la zone supralittorale du Pacifique du nord-ouest. L’isopode Ligia pallasii (Brandt, 1833), l’amphipode des rives rocheuses Traskorhychia traskana (Stimpson, 1857) et l’amphipode des plages sablonneuses Megarhychia californiana (Brandt 1851) ont des préférences alimentaires semblables, ce qui semble indiquer que les préférences alimentaires dépendent des caractéristiques des algues plutôt que d’adaptations particulières de ces herbivores spécifiques. Aucune caractéristique ne pouvait établir une distinction claire entre les algues très appréciées et les algues peu appréciées, bien que le pH et les contenus phénoliques ne soient avérés importants chez deux algues à défense chimique (Desmarestia sp. et Fucus sp., respectivement). Les préférences alimentaires de L. pallasii sont affectées par l’histoire de leur régime, mais ces effets sont mineurs comparativement aux effets des caractéristiques des algues. Les 3 consommateurs semblent préférer le varech (vieilles algues abandonnées par les vagues) que les algues fraîches des mêmes espèces. Nos résultats semblent indiquer que le contenu élevé en minéraux et en matières organiques du varech influence fortement les préférences alimentaires de ces organismes, mais que la dureté et le contenu en sel et en azote ne comptent pas. La teneur réduite en substances de défense peut avoir rendu le varech plus appétissant que les algues fraîches dans le cas des deux espèces d’algues à système de défense chimique.

[Traduit par la Rédaction]

Introduction

Deposition of seaweeds onto the shore by waves and tides creates an energetic link between marine and terrestrial systems. In bays that concentrate floating debris, and small islands or peninsulas with a high edge:area ratio, marine subsidy of terrestrial food webs may be similar in magnitude to, or exceed, terrestrial production (Bustamante et al. 1995; Polis and Hurd 1996; Polis et al. 1997). The organisms that feed on stranded seaweeds (wrack), primarily amphipods, isopods, and flies, are potentially important agents mediating this subsidy (Koop and Field 1980, 1981; Venables 1981; Mclachlan 1985; Wildish 1988). Their population densities, behaviour, and feeding rates likely affect whether marine subsidies enter terrestrial food webs via predator (e.g., birds, semiterrestrial crabs, supralittoral beetles) or decomposer (e.g., bacteria, fungi) pathways, and how rapidly. Moreover, consumers’ feeding preferences (e.g., Carefoot 1973a; Koop and Field 1981; Robertson and Lucas 1983; Moore et al. 1995) may lead to different alga species being processed at different rates and (or) through different pathways (Craford 1984).

Processes analogous to the intertidal standing of seaweeds have been studied in other systems (Poist et al. 1997). In many low-order streams, input of leaf litter from trees is subsidized the food web (Cummins 1973; Cummins et al. 1989; Walla et al. 1999). Primary consumers of leaf litter in streams, such as Trichoptera and Diptera, influence its availability to secondary consumers and decomposers (Bärlöcher 1980; Graça 1993). Similarly, many terrestrial soil food webs are subsidized by leaf litter, and incorporation of leaf litter into soil food webs is mediated by the activity of earth-
worms, isopods, and millipedes, which feed upon fallen leaves (Slapokas and Granhall 1991; Coleman and Crossley 1996; Heneghan et al. 1999). In salt marshes in the southeastern U.S.A., senescent leaves of the dominant marsh plant, Spartina alterniflora, are shredded by the gastropod Littoraria irrorata and the amphipod Uholcerestia spartinophila before entering the benthic food web (Newell and Bärlocher 1993; Newell 1996). In all these systems, the initial processing of dead plant material by a variety of invertebrate consumers is a key process mediating the speed and manner in which the plant material enters the food web. The factors underlying feeding choices of consumers of leaf litter have been examined in terrestrial and aquatic systems (e.g., Ward and Cummins 1979; Rushton and Hassall 1983a, 1983b; Dudgeon et al. 1990), but in comparison, the factors mediating feeding choices by consumers of stranded seaweeds are poorly understood (Carefoot 1973a; Koop and Field 1981; Robertson and Lucas 1983; Agnew and Moore 1986).

We examined 3 consumers of wrack seaweed in the high intertidal and supralittoral zones of the Pacific Northwest coast of North America. In these systems, the isopod Ligia pallasi and various amphipods are among the major consumers of wrack. We worked primarily with L. pallasi (hereinafter Ligia), but also conducted comparative studies with the rocky-shore amphipod Traskorhestes traskiana (hereinafter Traskorhestes), and the sandy-beach amphipod Megalorchestes californiana (hereinafter Megalorchestes). We focused on four questions: (1) Which seaweeds are the most preferred foods? (2) Do feeding preferences depend on the recent feeding history of the consumer? (3) Do consumers prefer fresh or wrack seaweeds? (4) What characteristics of fresh and wrack seaweeds are responsible for observed feeding preferences?

Methods

Study site and species

All work was conducted at the Bamfield Marine Station, Bamfield, British Columbia (125°W, 49°N), in July 1998. Animals were hand-collected from nearby beaches. All 3 crustacean species that we studied are sexually dimorphic, males being larger than females. Ligia is a large (up to 6 cm long, 2 g live mass) nocturnally active isopod common in the supralittoral zone of rocky beaches from the Aleutian Islands in Alaska to northern California, U.S.A. Its biology has been extensively studied (Carefoot 1973a, 1973b; Carefoot and Taylor 1995; Carefoot et al. 1998, 2000).

Ligia was divided into four groups, and we measured 20 representative individuals of each; large males ranged from 30 to 40 mm, medium-sized males from 22 to 31 mm, females from 22 to 31 mm, and gravid females from 22 to 27 mm in length. Small individuals were not used. Traskorhestes is common in the supralittoral zone of rocky beaches from the Aleutian Islands to Baja California, Mexico (Koch 1989a, 1989b, 1990), and at our study site typically co-occurred with Ligia. We used individuals measuring 12–19 mm in length without sexing them. Megalorchestes is common in the supralittoral zone of sandy beaches from British Columbia, Canada, to southern California, U.S.A. We used individuals 13–17 mm in length without sexing them.

Live seaweeds were collected from intertidal or shallow subtidal zones, held in running seawater in the laboratory, and used within 48 h of collection. Wrack was collected from the higher strand lines on rocky and sandy beaches. In the context of this paper, wrack refers to seaweeds that were stranded in the high-intertidal zone and desiccated by exposure to air and sun. An immediate consequence of desiccation is a large increase in the relative dry mass of organic matter and minerals, most notably NaCl and CaCO3. Wrack traits could also be modified by UV exposure and microbial activity. Variability in microhabitat (e.g., sun versus shade, intertidal elevation, size of wrack clump) and time of exposure is likely to create great variability in wrack traits. To standardize our wrack specimens as much as possible, we collected only thalli that were desiccated and bleached (i.e., clearly distinguishable from fresh seaweeds), but otherwise intact. We studied 1 green (Ulva sp., probably fenestrata), 4 red (Desmarestia sp., probably ligulata; Chondracanthus (= Gigartina) sp., probably exasperatus; Mazzella (= Iridea) sp., probably splendens; Porphyra sp.), and 4 brown (Costaria costata (Turner) Saunders; Fucus sp., probably gardneri; Macrocystis integrifolia Bory; Nereocystis betkeana (Mertens) Postels and Ruprecht) seaweeds, all chosen because they were common as wrack. Seaweeds are referred to hereinafter by their generic names.

General methods

Animals were held individually in 200-mL containers with loose-fitting lids. Fresh seawater was available in a 3-mL dish. Ventilation was provided by the loose fit of the lid and by opening the lid twice daily to check the animal. Seaweeds for feeding assays were provided in standardized sizes by cutting discs from the blades with a cork borer. Unless otherwise noted, 21 mm diameter discs were used in feeding assays with large male Ligia and 14 mm diameter discs in all other assays. To standardize variation in body size and feeding rate, individual replicates of preference experiments were stopped when sufficient feeding had taken place to allow preferences to be discerned unambiguously (details of each experiment are provided below), and replicates in which animals did not feed within 3 days were dropped. When assays were stopped, the percentage of each disc that was eaten was visually estimated to the nearest 10%. Proportional data were arcsine square root transformed to improve normality before analysis.

Preferences among fresh seaweeds

To determine preferences of male (medium-sized) and female Ligia and Traskorhestes for different seaweeds, we offered each group two different arrays of 5 seaweed species each. Macrocystis was included in each array to provide a standard for comparing arrays. Thus, the first array consisted of Nereocystis, Macrocystis, Ulva, Mazzella, and Fucus and the second array of Porphyra, Macrocystis, Costaria, Desmarestia, and Chondracanthus. Assays were allowed to continue for up to 3 days, discs being progressively removed when ≥70% eaten in order to determine the rank order of preference for all 5 seaweeds in each array. Because of the difficulties inherent in statistically analyzing the results of multiple-choice feeding assays, we present the results (mean rank ± 1 SE) without formal statistical analysis.

Effect of feeding history on feeding preferences of Ligia

To determine if feeding preferences changed as a function of feeding history, we maintained individual male (medium-sized) and female Ligia on monospecific diets of Macrocystis, Nereocystis, and Ulva for 4 days (pre-diet). These seaweeds were chosen because all were common as wrack and preference for all was high or medium (see Results). After 4 days, animals were presented with a choice between a single disc of each of the 3 species. Replicates were stopped when one of the discs was ≥70% eaten or after 3 days. For each animal we calculated the proportion of the diet made up of each seaweed. ANOVA was used to compare the percentage of each seaweed eaten by animals from the 3 feeding histories. Since the three ANOVAs were run on data collected from the same experiment, they were not independent, and significance levels should be interpreted with caution.

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Preferences for fresh versus wrack seaweeds

Organisms feeding on stranded seaweeds will often have a choice between feeding on material that has recently been deposited ("fresh") or material that has been exposed for days or weeks ("wrack"). To determine if *Ligia* (large males, females, and gravid females) preferred fresh or wrack seaweeds, we conducted experiments with 7 seaweeds (*Macrocystis, Nereocystis, Costaria, Fucus, Ulva, Desmarestia, Mazzella*) in which we offered individual *Ligia* a choice between fresh and wrack forms of the same species. Replicates were stopped when one of the discs was ≥50% eaten or after 3 days. To compare the results from *Ligia* with those from other supralitoral herbivorous crustaceans, we performed identical experiments using *Traskorchestia* and *Megalorchestia*. Data were analyzed with paired *t*-tests.

Effect of salt, organic, and CaCO$_3$ contents on feeding preferences

Additional assays examine the effects of salt, organic, and CaCO$_3$ contents on feeding by *Ligia* (large males, small males, and females) and *Traskorchestia* were conducted by adding these components to a base diet of powdered seaweed that was reconstituted in an agar matrix. We reduced *Macrocystis* to a powder by drying *Macrocystis* wrack at 60°C and grinding it with a mortar and pestle. Agar (5% mass/volume) was dissolved in heated distilled water and *Macrocystis* powder was added at 10% (mass/volume), approximating the dry mass content of fresh *Macrocystis*. Additional dietary components to be tested were mixed into the cooling agar before it set. The mixture was poured into inverted petri-plate lids, and the petri-plate bottoms were gently set into the lid in order to press the mixture to a constant thickness (about 4 mm). After setting, individual discs (8 mm in diameter) were removed using a cork borer. Assays with agar discs were terminated after 2 days; feeding was scored by estimating consumption of each disc to the nearest 10% and data were analyzed using paired *t*-tests.

Salt (NaCl) was added at 3% or 9% (mass/volume) to approximately double or quadruple the salt content, as would happen when wrack desiccates. Consumers were offered a choice between the base diet and one of the salt-enriched diets. To determine if the availability of fresh water affected choice, assays were conducted with either distilled water or no water available.

The organic content was increased by adding an isopod chemical diet (0.2% NaCl, 5% total minerals; *Zimmer* 1999, modified after *Carefoot* 1984) at 10% mass/volume, to approximately double the organic content without markedly increasing the salt content. Animals were offered a choice between the base diet and the diet with enriched organic content.

The CaCO$_3$ content was increased by adding powdered calcite at 1.3% mass/volume, in order to approximately triple the calcium content of typical noncalcified seaweeds. Since calcium is essential for molting in *Ligia*, we took care to use only animals in the "intermoult" stage (e.g., showing no signs of calcite deposits in the anterior thorax indicative of impending moult; *Ziegler* et al. 2000). Individual *Ligia* were offered a choice between the base diet and the diet with additional CaCO$_3$.

Characteristics of fresh and wrack seaweeds

To explore further the factors that might determine feeding preferences of *Ligia* and the amphipods, we measured pH, toughness, nitrogen, carbon, and water contents, and concentrations of phenolic compounds in fresh and wrack forms of different seaweed species. Since all the traits we measured, including concentrations of phenolics, are likely to vary among parts of the algal thallus (*Tugwell and Branch* 1989), we collected material from the same parts of the thallus that we used for feeding experiments. We measured pH by grinding seaweeds with a mortar and pestle and pressing a pH test strip (range 1–7, precision 0.5) against the macerated sample. If wrack was too dry to obtain a reading, a minimal amount of distilled water was added during grinding. The pH data were not analyzed statistically because variability was zero among replicates of many seaweeds. We measured toughness using standard penetrometer techniques (*Feeny* 1970; *Littler and Littler* 1980; *Penning and Paul* 1992): we measured the force in newtons required to punch a 1.9 mm diameter rod through seaweed thallus clamped between Plexiglas plates. Total nitrogen and carbon were measured using a Carlo Erba NA-1500 NCS Analyzer. The percentage of water in fresh and wrack seaweeds was determined by weighing samples before and after drying to a constant mass. The concentration of phenolics in fresh and wrack seaweeds was determined using a Folin–Denis assay (*Swain and Hillis* 1959). Phloroglucinol (Sigma, St. Louis, Missouri; lot 116H3717) served as a standard.

Results

Preferences among fresh seaweeds

Male and female *Ligia* had similar preferences for fresh seaweeds in the first-choice array (Fig. 1A). *Nereocystis* and *Macrocystis* ranked highest in preference, *Ulva* was intermediate, and *Mazzella* and *Fucus* ranked lowest. The preferences of *Traskorchestia* were similar to those of *Ligia* except that *Ulva* fell among the low-preference seaweeds (Fig. 1A).

Male and female *Ligia* again had similar preferences for seaweeds in the second-choice array (Fig. 1B). *Porphyra* and *Macrocystis* ranked highest in preference, *Costaria* was intermediate, and *Desmarestia* and *Chondracanthus* ranked lowest. The preferences of *Traskorchestia* were similar to those of *Ligia* except that *Costaria* fell among the high-preference seaweeds (Fig. 1B).

Effect of feeding history on feeding preferences of *Ligia*

Feeding preferences changed as a result of feeding history; however, differences between feeding histories were small and difficult to interpret (Fig. 2). Preferences for *Macrocystis* and *Nereocystis* did not differ by sex of *Ligia*, and so are presented for the sexes pooled. The results for *Ulva* indicated a sex by pre-diet interaction and so are presented both pooled and by sex. Overall, *Nereocystis* was eaten in large amounts (ca. 70% of the diet), whereas *Macrocystis* and *Ulva* each comprised only about 15% of the diet. Compared with the large differences between seaweeds, the effects of the pre-diet were modest. Consumption of *Macrocystis* was lowest for animals fed the *Macrocystis* pre-diet and highest when *Macrocystis* was novel. Consumption of *Nereocystis* was lowest for animals fed the *Ulva* pre-diet and highest for animals fed the *Macrocystis* pre-diet. Consumption of *Ulva* differed by sex. Males ate the least *Ulva* if fed the *Nereocystis* pre-diet, but females ate the least *Ulva* if fed the *Macrocystis* pre-diet.

Preferences for fresh versus wrack seaweeds

Overall, all consumers preferred wrack over fresh seaweeds of the same species; however, the strength of this preference varied among consumers and seaweeds (Fig. 3). Large male *Ligia* preferred wrack over fresh for all seaweeds except *Mazzella*. Large male *Ligia* offered *Desmarestia* were commonly seen hanging upside down from the lid of their containers, a behaviour not seen in individuals offered other seaweeds. Female *Ligia* refused to eat *Desmarestia* or *Mazzella*, and significantly preferred wrack over fresh only for *Fucus* (and perhaps *Ulva*, *P* = 0.057), but in all other cases.

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Fig. 1. Feeding preferences (mean rank ± 1 SE) of *Ligia* and *Traskorchestia* for two arrays of fresh seaweeds; *n* = 10 (male *Ligia*), 16 (female *Ligia*), and 15 (*Traskorchestia*) for the top array and *n* = 14, 12, and 11, respectively, for the bottom array.

displayed a nonsignificant trend toward eating more of the wrack than of the fresh seaweeds. Gravid female *Ligia* refused to feed in most assays (*Macroystis, Costaria, Fucus*), significantly preferred wrack over fresh *Ulva*, and displayed no preference for wrack versus fresh *Nereocystis*. *Traskorchestia* preferred wrack over fresh of all 7 seaweeds. *Megalorchestia* preferred wrack over fresh *Nereocystis, Costaria*, and perhaps *Macroystis (P = 0.055)*, and refused to eat *Desmarestia*.

**Effect of salt, organic, and CaCO₃ contents on feeding preferences**

The effect of salt (NaCl) on feeding depended both on its concentration and on the availability of water (Fig. 4). When distilled water was available to animals (Fig. 4A), most assays indicated no significant selection between the control and salt-enriched diets; however, one assay indicated a preference for the salt-enriched diet (small male *Ligia, 3%*) and another indicated avoidance of the salt-enriched diet (*Traskorchestia, 9%*). In contrast, in the absence of water, four comparisons indicated avoidance of the salt-enriched diet (Fig. 4B, large male *Ligia, 9%*; all *Ligia* combined, 9%; *Traskorchestia, 3 and 9%*), and none indicated a preference for it.

The organic-enriched diet was strongly preferred by *Ligia* over the control diet in 3 of 3 assays (Fig. 4C). Similarly, *Ligia* strongly preferred the CaCO₃-enriched (+1.3% CaCO₃) diet over the control diet (Fig. 4D).

**Characteristics of fresh and wrack seaweeds**

In most cases, seaweed pH was between 5.3 and 6.5, and differed by ≤1 unit between fresh and wrack forms (Table 1). The exception was *Desmarestia*, which was highly.
Fig. 2. Effects of feeding history on feeding preferences of Ligia; since these effects are statistically significant but relatively modest, data (proportion of a seaweed in the diet; mean ± 1 SE) from animals with each diet history are grouped according to alga species. Data are pooled by sex of Ligia for all 3 alga species, and also separately by sex for Ulva, which was the only alga for which there was a significant pre-diet by sex interaction; n = 26 (Macrocystis pre-diet), 17 (Nereocystis pre-diet), and 24 (Ulva pre-diet, 12 males and 12 females).

Seaweeds offered in assay

Acidic (pH 1.5) when sampled fresh, but considerably less so (pH 4.5) when sampled as wrack.

Wrack was significantly tougher than fresh in 6 of 9 seaweed species tested, often markedly so; in the other 3 species, wrack and fresh did not significantly differ in toughness (Table 1).

The nitrogen content of wrack was significantly lower than that of fresh seaweeds (on a dry mass basis) in 4 of 5 species that were tested; in the other case wrack and fresh did not differ significantly (Table 1). In 3 of 5 species, the carbon:nitrogen ratio of wrack was significantly higher than that of fresh seaweeds; in the other 2 cases wrack and fresh did not differ significantly (Table 1).

Fresh seaweeds ranged from 75 to 90% water, depending on species. For all species except Chondracanthus, wrack was significantly desiccated, ranging from 15 to 23% water.

The concentration of phenolics in fresh seaweeds was high for Fucus (6% dry mass) and less than 1% for all other species (Table 1). In 3 of 9 species (including Fucus) the concentration of phenolics was lower in wrack than in fresh seaweeds, and in 3 species it was higher.

Discussion

Our results indicate that the supralittoral invertebrates which we studied had strong feeding preferences among seaweeds and generally preferred wrack over fresh seaweeds. The results were largely consistent among consumer species. No single trait clearly distinguished high- from low-preference seaweeds; however, the preference for wrack was likely due at least in part to desiccation, which concentrated the organic matter within a given volume of food. We will first consider the preferences of Ligia and amphipods for different fresh seaweeds, and then consider preferences for fresh versus wrack seaweeds.

Preferences for fresh seaweeds

Feeding preferences for fresh seaweeds were similar between the sexes of Ligia and between Ligia and Traskorchestia. A high preference for Nereocystis and a low preference for Fucus were consistent with earlier studies of feeding preferences of L. pallasi (Carefoot 1973a). Moreover, the preferences of Ligia and Traskorchestia were broadly comparable to feeding preferences of other generalist feeders on seaweeds in the Pacific Northwest (Watano 1984; Steinberg 1985).

None of the traits that we measured (pH, toughness, nitrogen content, carbon:nitrogen ratio, water content, or concentration of phenolics) differed consistently between high-preference (Nereocystis, Macrocystis, Porphyra) and low-preference seaweeds (Desmarestia, Fucus, Mazzaella, Chondracanthus) (Ulva and Costaria are excluded because of intermediate preference rankings; t tests, P ≥ 0.30 in all cases). In previous studies with isopods also, there was little success in explaining dietary choices (Carefoot 1973a; Koop and Field 1981; Arronte 1990; Dudgeon et al. 1990), and in general, predicting the feeding preferences of marine herbivores has proved to be a challenging task (Penning and Paul 1992; Penning et al. 1998). This may stem in part from a general inability on our part to measure key traits that determine feeding preferences (e.g., specific nutritional requirements),
or it may be that feeding preferences are based on the simultaneous integration of multiple plant traits, with the consequence that in studies such as ours, with a modest number of diets, we are unable to discern patterns clearly. For example, while the low preference for Desmarestia was likely due to the low pH of this seaweed, pH was probably irrelevant to preferences for the other diets studied. Similarly, the high concentration of phenolics in Fucus may have deterred feeding on this seaweed, but variation in the relatively low concentrations of phenolics found in the other seaweeds may have been irrelevant to feeding preferences (Steinberg 1985). It is clear that if half a dozen or more traits combine to affect feeding preferences, the importance of each trait will only be apparent in a correlative study if a large number of plant species are studied.

If mixed diets are superior to single foods, feeding choices may depend on prior feeding history (Westoby 1978; Bernays and Bright 1991; Pennings et al. 1993; Bernays et al. 1994).
Fig. 4. Effect of salt (NaCl), organic, and CaCO₃ contents on feeding preferences of Ligia and Traskorchestia. Data (percentage of food disc eaten) are given as the mean ± 1 SE; sample sizes and P values (paired t tests) are indicated above the bars. Percentages under the histograms in A and B indicate the salt enrichment (percent dry mass NaCl) of the treatment diet over the control diet.

At least two studies have documented such patterns in isopods (Rushton and Hassall 1983a; Dudgeon et al. 1990). Our results showed that previous feeding history did affect feeding choices made by Ligia, but these effects were minor compared with differences among food types. Since we only examined the effects of 3 diets, all of which consisted of high- or intermediate-preference foods, it may be that studies with a wider range of diets would reveal larger effects of diet history on feeding preferences of Ligia.

Preferences for fresh versus wrack seaweeds
Both sexes of Ligia and the two amphipod species showed consistent preferences for wrack over fresh seaweeds of the same species. These results were consistent across all alga
Table 1. Characteristics of fresh and wrack seaweeds.

<table>
<thead>
<tr>
<th>Species</th>
<th>pH</th>
<th>Toughness (newtons)</th>
<th>Nitrogen (% dry mass)</th>
<th>C:N ratio</th>
<th>Water content (% of total mass)</th>
<th>Phenolics (% dry mass)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>n</td>
<td>6.82 (1.21, 10)</td>
<td>2.13 (0.04, 4)</td>
<td>12.9 (0.27, 4)</td>
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<tr>
<td>Chondracanthus sp.</td>
<td>Fresh</td>
<td>6.3</td>
<td>0.3</td>
<td>3</td>
<td>28.22 (0.99, 7)</td>
<td>nd</td>
</tr>
<tr>
<td></td>
<td>Wrack</td>
<td>5.3</td>
<td>0.2</td>
<td>3</td>
<td>6.03 (0.36, 10)</td>
<td>2.13 (0.08, 6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5.04 (0.88, 8)</td>
<td>nd</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>P = 0.20</td>
</tr>
<tr>
<td>Costaria costata</td>
<td>Fresh</td>
<td>6.0</td>
<td>0.0</td>
<td>3</td>
<td>2.04 (0.17, 9)</td>
<td>nd</td>
</tr>
<tr>
<td></td>
<td>Wrack</td>
<td>4.5</td>
<td>0.8</td>
<td>3</td>
<td>16.04 (1.65, 8)</td>
<td>1.36 (0.03, 6)</td>
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<tr>
<td>Desmarestia sp.</td>
<td>Fresh</td>
<td>1.5</td>
<td>0.0</td>
<td>3</td>
<td>8.88 (1.24, 10)</td>
<td>1.04 (0.06, 6)</td>
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<tr>
<td></td>
<td>Wrack</td>
<td>5.5</td>
<td>0.0</td>
<td>3</td>
<td>8.12 (1.02, 10)</td>
<td>1.21 (0.09, 6)</td>
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<tr>
<td>Fucus sp.</td>
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<td>5.5</td>
<td>0.0</td>
<td>3</td>
<td>1.87 (0.09, 6)</td>
<td>1.15 (0.08, 6)</td>
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<tr>
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<td>Wrack</td>
<td>6.2</td>
<td>0.2</td>
<td>3</td>
<td>4.24 (0.50, 10)</td>
<td>1.04 (0.06, 6)</td>
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<tr>
<td>Macrocytis integrifolia</td>
<td>Fresh</td>
<td>5.3</td>
<td>0.2</td>
<td>3</td>
<td>8.88 (1.24, 10)</td>
<td>1.36 (0.03, 6)</td>
</tr>
<tr>
<td></td>
<td>Wrack</td>
<td>5.5</td>
<td>0.0</td>
<td>3</td>
<td>8.12 (1.02, 10)</td>
<td>1.21 (0.09, 6)</td>
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<tr>
<td>Mazzella sp.</td>
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<td></td>
<td>Wrack</td>
<td>5.5</td>
<td>0.3</td>
<td>3</td>
<td>4.14 (0.61, 10)</td>
<td>1.51 (0.10, 5)</td>
</tr>
<tr>
<td>Nereocystis luetkeana</td>
<td>Fresh</td>
<td>6.3</td>
<td>0.2</td>
<td>3</td>
<td>2.70 (0.12, 10)</td>
<td>2.35 (0.06, 6)</td>
</tr>
<tr>
<td></td>
<td>Wrack</td>
<td>6.0</td>
<td>0.0</td>
<td>3</td>
<td>3.47 (0.60, 8)</td>
<td>nd</td>
</tr>
<tr>
<td>Porphyra sp.</td>
<td>Fresh</td>
<td>5.3</td>
<td>0.2</td>
<td>3</td>
<td>0.78 (0.15, 10)</td>
<td>1.69 (0.05, 6)</td>
</tr>
<tr>
<td></td>
<td>Wrack</td>
<td>6.5</td>
<td>0.0</td>
<td>3</td>
<td>1.25 (0.12, 12)</td>
<td>0.72 (0.15, 4)</td>
</tr>
<tr>
<td>Ulva sp.</td>
<td>Fresh</td>
<td>5.3</td>
<td>0.2</td>
<td>3</td>
<td>0.78 (0.15, 10)</td>
<td>1.69 (0.05, 6)</td>
</tr>
<tr>
<td></td>
<td>Wrack</td>
<td>6.5</td>
<td>0.0</td>
<td>3</td>
<td>1.25 (0.12, 12)</td>
<td>0.72 (0.15, 4)</td>
</tr>
</tbody>
</table>

Note: nd, not done. P values in boldface type are significant.

species, and are in agreement with more limited data obtained from other herbivorous crustaceans (Robertson and Lucas 1983; Agnew and Moore 1986). In general, supralittoral crustaceans probably have varied diets, feeding facultatively on fresh and wrack seaweeds and carrion, depending on the availability of each, which is likely to vary spatially and temporally (Carefoot 1973a; Agnew and Moore 1986; Willows 1987). The preference for wrack over fresh seaweeds shown here may be mediated by a number of plant traits. Live and decomposing plant material is likely to vary in toughness, nutritional composition, and concentrations of nutrients, water, minerals, and secondary metabolites (McClougherty et al. 1985; Gallardo and Merino 1993; Vitousek et al. 1994; Wood et al. 1995). It is reasonable to hypothesize that the increased toughness, reduced nitrogen content, and increased salt content of wrack are likely to reduce its palatability compared with that of fresh seaweeds. On the other hand, the increased ratio of organic matter to water and the reduced content of unpalatable secondary metabolites might make wrack more palatable than fresh seaweeds. We will consider each of these factors in turn.

Feeding studies with a variety of invertebrate consumers have indicated that toughness reduces palatability, presumably by increasing the difficulty of removing material (Pennings and Paul 1992; Pennings et al. 1998). Our results indicated that wrack was tougher than fresh seaweeds for most seaweed species tested, therefore it should have been of lower, rather than higher, palatability to consumers. Robertson and Lucas (1983) and Agnew and Moore (1986) concluded that the decreased toughness of wrack is an important quality that increases its palatability to amphipods; however, they were working in lower intertidal habitats, where wrack remained better hydrated and therefore softer. In our experiments, we did not directly manipulate plant toughness (sensu Pennings and Paul 1992; Pennings et al. 1998). Had we done so, we expect that consumers would have preferred softer

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foods. Thus, in our experiments, Ligia and the amphipods likely preferred wrack because its other traits stimulated feeding more than the increased toughness deterred it.

Wrack and fresh seaweeds likely differ in nutritional quality in several ways. Decaying seaweeds are colonized by bacteria and fungi that may themselves be more digestible than fresh seaweed tissue (Wildish 1988; but see Robertson and Lucas 1983; Agnew and Moore 1986). Consumers of dead angiosperm leaves often preferentially consume areas heavily colonized by microorganisms and (or) perform better on “conditioned” leaves with high microbial content (Ward and Cummins 1979; Newell and Bärlocher 1993; Zimmer et al. 1996; Zimmer and Topp 1997). We have not examined the influence of microorganisms on subtle aspects of nutritional quality here, but we suggest that it deserves future study.

Even mild desiccation can reduce the protein content of some seaweeds (Renaud et al. 1990). In our study, nitrogen content was reduced in heavily desiccated wrack of 4 of 5 seaweed species tested, and the carbon:nitrogen ratio elevated in 3 of these cases. Since plant consumers are usually assumed to be nitrogen-limited, these results speak to wrack being an inferior food source to fresh seaweeds. Nevertheless, studies of consumers that feed on either living plants or litter typically reveal poor correlations between feeding preferences and nitrogen content (Ward and Cummins 1979; Rushton and Hassall 1983a; Pennings et al. 1998; Poore and Steinberg 1999), which suggests that other aspects of food quality are more important.

A major advantage of wrack as a food source may be its reduced water content. Assuming that the rate of intake of food is limited by its volume, a given volume of wrack will have several times the organic content of the same volume of fresh seaweed. In laboratory experiments, Ligia strongly preferred an artificial diet with doubled organic content/volume over a control diet, which suggests that they are responsive to the concentration of organics in their food. If the time available for feeding is limited (Carefoot et al. 1998), or if feeding exposes a consumer to predators, diets that allow rapid ingestion of organic matter should be strongly preferred. Studies with insects, however, have shown that although wilted and turgid leaves differ in palatability, wilted leaves are not always preferred, and the effects of reduced water content versus subtler changes in nutritional quality on palatability are not clear (Lewis 1982; Bernays and Lewis 1986).

In addition to concentrating nutrients, desiccation of seaweeds also concentrates salts. Since maintaining their osmotic balance is a problem for semiterrestrial crustaceans (Wildish 1988; Morriss 1989; Carefoot and Taylor 1995), and since dietary intake of salts is a major factor affecting their osmotic balance (Carefoot et al. 2000), it is reasonable to hypothesize that they avoid eating wrack because of its high salt concentration. Our results generally fail to support this hypothesis. Ligia in the field would typically have access to fresh water from dew and rainfall. Under similar conditions in the laboratory, feeding by Ligia and Traskorchestia was not affected by or was stimulated by doubled (control level + 3%) salt concentrations similar to those found in moderately desiccated seaweeds. Higher (control level + 9%) salt concentrations, such as might be found in severely desiccated wrack, did not affect feeding by Ligia but were avoided by Traskorchestia. In contrast, when animals were not provided with water, they generally avoided diets containing added salt. Work with other supralittoral crustaceans has similarly shown that diets with moderate to high salt levels are commonly preferred over diets low in salt (Wildish 1988; Pennings et al. 1998). These results suggest that the high salt concentrations found in desiccated wrack are unlikely to represent a negative stimulus to Ligia or Traskorchestia as long as a ready supply of fresh water is available. In support of this hypothesis, diet did not affect hemolymph osmolality in Ligia given access to fresh water in the laboratory (T.H. Carefoot, unpublished data). In contrast, if fresh water was not available, as might happen during an extended period without rainfall, or in more arid climates, higher salt concentrations in greatly desiccated wrack could be a negative stimulus to feeding by both isopods and amphipods. Under what conditions this negative stimulus would outweigh the positive stimulus of the coincidental increase in concentration of organic matter is an interesting question for future work.

Wrack is likely to differ from fresh seaweeds in the concentration of defensive compounds. The concentration of phenolics in fresh Fucus, which was the only alga with >1% phenolics, was twice that of Fucus wrack. Like other isopods, Ligia is capable of modest detoxification of phenolics (Zimmer and Topp 1998; Zimmer 1999; M. Zimmer, unpublished data), but diets high in phenolics are likely avoided or are detoxified only at some cost. Similarly, fresh Desmarestia was strongly acidic, but as wrack it was much closer to a neutral pH. Our observation that Ligia offered Desmarestia often rested upside down on the lid of their containers suggests that the acidic substrate was stressful. We speculate that long-term consumption of Desmarestia might be deleterious, as was found for other isopods fed acidic diets (Zimmer and Topp 1997). We did not quantify the concentrations of other secondary metabolites such as terpenes that might have been present in some of the red seaweeds, but it is reasonable to hypothesize that these compounds leach or break down relatively rapidly once the seaweeds begin to desiccate, since even mild desiccation and UV stress are known to increase palatability and reduce chemical defenses in seaweeds (Renaud et al. 1990; Cronin and Hay 1996; Trowbridge 1998). Several authors have speculated that isopods choose diets that enable them to avoid consuming large amounts of secondary metabolites (Robertson and Lucas 1983; Rushton and Hassall 1983b; Dudgeon et al. 1990). Although many of the seaweeds we studied are not known to contain secondary metabolites other than phenolics (Costaria, Fucus, Macroystis, and Nereocystis), or in any at all (Ulva), it is reasonable to hypothesize that breakdown of phenolics in Fucus and of other secondary metabolites in the red seaweeds might have contributed to the increased palatability of wrack. Confirmation of this hypothesis for Ligia will require studies that experimentally manipulate secondary metabolites, as Valiela et al. (1979) and Harrison (1982) did to explore consumption of senescent angiosperm leaves by leaf-litter detritivores.

Preferences for calcium-rich food

Many seaweeds are calcified, and a high CaCO₃ content deters feeding by many marine herbivores (Pennings and
Paul 1992; Hay et al. 1994; Schupp and Paul 1994). However, isopods, like all crustaceans, require calcium to replace that lost with each moult and to manufacture new cuticle (Carefoot 1993). Since Ligia typically eat their exuviae (at least in laboratory culture), and since their biphasic moulting process allows most calcium to be recycled between the posterior and anterior part of the body, actual calcium losses during moulting may be small (Carefoot 1993; Steel 1993; Ziegler et al. 2000). Nevertheless, additional calcium is needed for growth, and since Ligia rarely enter seawater, much of this calcium is likely obtained through the diet (Carefoot and Taylor 1995). In laboratory culture, most Ligia maintained for 50 weeks on an artificial holodic diet deficient in calcium died within a few weeks and never successfully moulted (Carefoot 1984). Surprisingly, animals fed a diet greatly enriched in calcium also showed poor survival and growth, possibly because of an imbalance between phosphorus and calcium (Carefoot 1984). Our results indicate that in short-term preference experiments, these supralittoral crustaceans strongly prefer a Macrocystis-based diet modestly enriched in calcium over a control diet. The most reasonable interpretation of these results is that Ligia in the field are typically calcium-deprived, and (or) that the Macrocystis diet alone is deficient in calcium. In this regard, the Dudgeon et al. (1990) observed that 4 species of isopods from Hong Kong that were offered litter from 8 plant species all fed heavily on a species with an unusually high calcium content. The extent to which a drive for calcium affects the feeding preferences and (or) behaviour of Ligia and other terrestrial crustaceans deserves further attention.

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